

# A New Subfamily of the Addisoniidae Associated with Cephalopod Beaks from the Tropical Southwest Pacific, and a New Pseudococculinid Associated with Chondrichthyan Egg Cases from New Zealand (Mollusca: Lepetelloidea)

by

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**Abstract.** *Helicopeltinae*, a new subfamily of the Addisoniidae, is proposed for a group of minute deep-sea gastropods found living and feeding on detrital cephalopod beaks from the Chesterfield Plateau and southern New Caledonia. The type species of *Helicopelta* gen. nov., *H. rostricola* sp. nov., uniquely combines an operculate, coiled shell similar to that in *Choristella* Bush, 1987 (Choristellidae), a horseshoe-shaped shell muscle characteristic of a limpet, a radula similar to that in Addisoniidae but with more numerous marginal teeth and non-homologous primary rasping teeth, a large left-centered gill, and a copulatory organ that is situated on the left side instead of the right as in all other members of the Lepetelloidea. A second (unnamed) species of *Helicopelta* is recorded from off southern New Caledonia. The opportunity is taken to describe a new limpet of the genus *Tentaoculus* Moskalév, 1976, from New Zealand that lives and feeds within spent chondrichthyan egg cases, the first record of a pseudococculinid from this habitat. Radulae of *Teuthirostria cancellata* Moskalév, 1976, and of species of *Addisonia*, *Choristella*, and *Bathysciadium* are illustrated and discussed.

## INTRODUCTION

During the last 25 years, there has been a dramatic increase in knowledge of the systematics and anatomy of the Cocculinoidea and Lepetelloidea (reviewed by Haszprunar, 1988b). In this period the number of families has swelled to 10, and the number of genera and subgenera to 37, while the number of known species has substantially increased. These animals live and feed on a variety of exotic substrata, including empty polychaete (*Hyalinoecia*) tubes, the carapaces of living deep-sea Lithodidae (Crustacea), egg cases of sharks and skates (Chondrichthys), detrital cephalopod beaks, and decaying whale and fish bones, as well as terrestrial and littoral plant remains that have sunk to the deep-sea floor, such as wood, algal holdfasts and seagrass (reviewed by Haszprunar, 1988b). The Pyropeltidae (McLean & Haszprunar, 1987) and a pseudococculinid (McLean, 1991) have been recorded from sulphide crusts at hydrothermal vents on the East Pacific Rise. Warén (1993) has recently recorded a bathysciadiidlike limpet that lives and feeds on the periostracum of

a species of *Capulus* (Gastropoda, Capulidae). Most species are restricted to a particular substratum type.

In this paper I introduce a new subfamily of the Addisoniidae for coiled species that live on detrital cephalopod beaks, and a pseudococculinid that lives and feeds within spent skate egg cases.

**Abbreviations:** AMS, Australian Museum, Sydney; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington.

## SYSTEMATICS

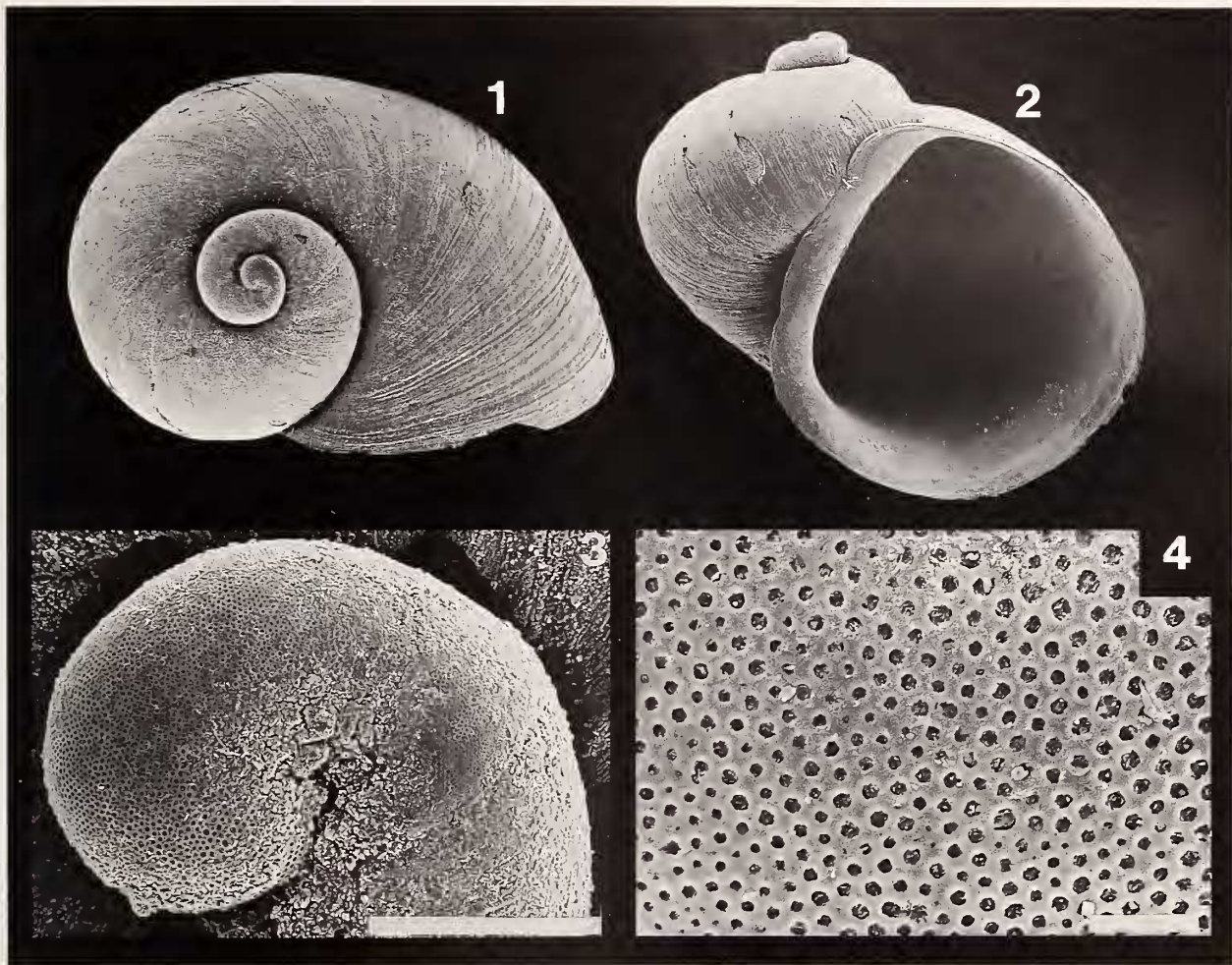
Order Archaeogastropoda Thiele, 1925

Superfamily LEPETELLOIDEA Dall, 1892

Family ADDISONIIDAE Dall, 1882

**HELICOPELTINAE** subfam. nov.

**Diagnosis:** Shell up to 1.90 mm wide, turbiniform, operculate; protoconch densely and minutely pitted, slightly



Explanation of Figures 1 to 4

Shell of holotype of *Helicopelta rostricola* Marshall, gen. nov., sp. nov., Chesterfield Plateau, Coral Sea, 700–685 m. Figures 1, 2. Whole shell (width 1.90 mm). Figure 3. Protoconch. Figure 4. Enlargement of protoconch sculpture. Scale bar 3 = 100  $\mu$ m, 4 = 10  $\mu$ m.

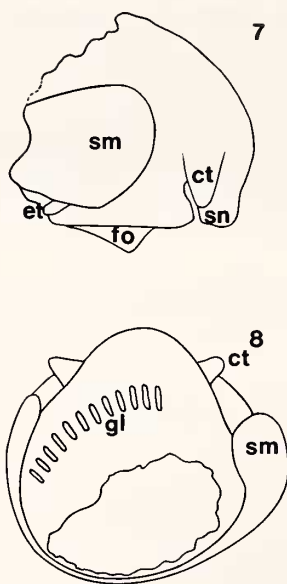
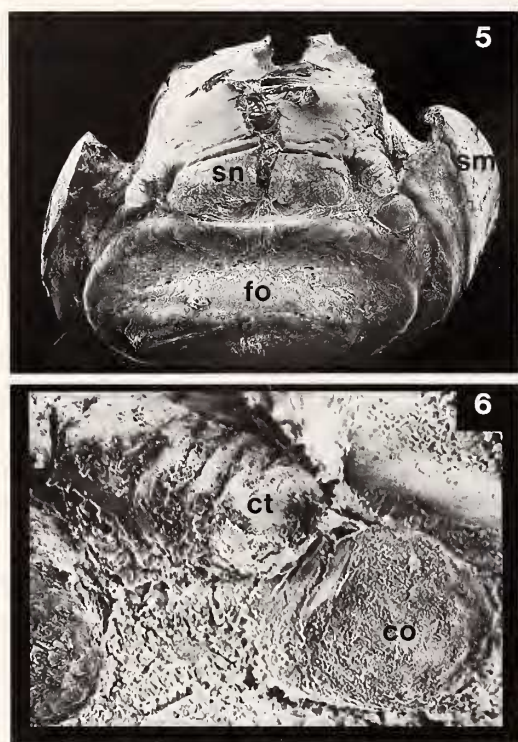
tilted; teleoconch essentially smooth. Copulatory organ beside left cephalic tentacle, hemispherical (opening not detected); large gill comprising a row of leaflets centered left of body midline; cephalic tentacles without papillae; two posterior epipodial tentacles; shell muscle horseshoe-shaped, uninterrupted, very wide. Operculum thin, chitinous. Radula 11 + 5 + 1 + 5 + 11, central tooth scalelike, laterals 1–3 tilelike, lateral 4 small, lateral 5 and marginal 1 broadest, marginal 1 longest; lateral 5 with small cusp at inner end, broad outer part tightly interlocked with base of marginal 1. Marginal 1 with bluntly angulate or rounded cusps, marginal basal plates scalelike, outer marginal teeth (10 pairs) relatively very small, slender, cutting areas finely serrate. Internal anatomy unknown.

**Remarks:** The type species of *Helicopelta* gen. nov. (Figures 1–8, 13–18) differs from all hitherto known members

of the Cocculinoidea and Lepetelloidea in having an operculate coiled shell (as in Choristellidae) coupled with a shell muscle characteristic of a limpet, and in having the copulatory organ on the left side instead of the right. The radula (Figures 13–18) uniquely combines central and lateral teeth similar to those of Addisoniidae (Figures 19–21) with multiple marginal teeth as in Cocculinoidea and Lepetelloidea with fully rhipidoglossate dentition (Cocculinidae, Pyropeltidae, Pseudococculinidae, Osteopeltidae), though the marginals are reduced in size and number and are evidently vestigial. The gill is large and most closely resembles those in *Addisonia* Dall, 1882, and Choristellidae, particularly the latter in being left rather than right-centered.

*Helicopelta* is clearly referable to the Lepetelloidea rather than the Cocculinoidea because (1) the gill comprises a row of leaflets rather than a simple fold, (2) the





Explanation of Figures 5 to 8

Animal of holotype of *Helicopelta rostricola* Marshall, gen. nov., sp. nov. Figures 5, 6. Critical point dried animal after extraction of radula. Figures 7, 8. Profile (7) and dorsal view (8) (posterior part of animal torn away); ct, cephalic tentacle; co, copulatory organ; et, epipodial tentacle; fo, foot; gl, gill leaflets; sm, shell muscle; sn, snout. Specimen width (Figures 5, 6) 1.20 mm.

shell muscle is not divided into discrete bundles, and (3) the radula is somewhat similar to that in Addisoniidae. The only other members of the Lepetelloidea (or Coccu-linoidea) with a coiled shell and that have an operculum in the adult stage are the choristellids (McLean, 1992). No weight is assigned to the presence of an operculum in the adult, because one is present in larval Patellogastro-poda (Lindberg, 1981) and has been observed in larval *Lepetella* Verrill, 1880 (A. Warén, personal communication). Choristellids differ in having jaws, a relatively small (left) shell muscle attached to the columella, and an es-sentially smooth protoconch, while a grooved right cephalic tentacle functions as the copulatory organ. Their radulae, moreover, are entirely different (compare Figures 13–18 with Figure 22), though both types are evidently derived by arrested development of and differential modification from a common, fully rhipidoglossate radular plan similar to that in Pseudococculinidae (Figures 27, 28), which is considered to be the primitive condition among Coccu-linoidea and Lepetelloidea (Haszprunar, 1988a, b). Re-grettably no complete animal of *Helicopelta* is yet avail-able for sectioning and anatomical comparison with other members of the Lepetelloidea. It remains to be determined, for example, on what side the gonads are and how they are collected to the copulatory organ.

The central and inner five lateral radular teeth in *Ad-disonia* and *Helicopelta* are more similar to each other than to those of any other family of the Lepetelloidea, and suggest that the two groups have a common stem group. *Addisonia* species differ, however, in having a patelliform shell and the gill on the right side, and in that the right cephalic tentacle functions as the copulatory organ. Apart from the presence of more numerous marginal teeth, the radula in *Helicopelta* differs from that in *Addisonia* in the shapes and homologies of the largest teeth (Figures 16, 19, 21). Unlike *Helicopelta*, in which the sixth tooth out-ward from the central tooth (here interpreted as marginal 1) is by far the largest and is thus clearly the primary rasper, tooth 6 (marginal 1) in *Addisonia* is situated beneath the large seventh and eighth elements (marginals 2 and 3), which are obviously the primary rasps in this genus. Note that McLean (1985) and Dantart & Luque (1994) recorded only 15 teeth per transverse row in the *Addisonia* species they examined, whereas Anders Warén (personal communication) has found that these same species actually have 19 teeth ( $9 + 1 + 9$ ) as in the one illustrated here (Figures 19–21) (teeth 7 and 8 are typically obscured by the adjacent inner teeth through shrinkage of the basement membrane). The protoconch in *Addisonia*, as interpreted by Dantart & Luque (1994, figs. 73–76), differs markedly from that in *Helicopelta* in being reticulately sculptured, and in having a fused, narrowly tapered instead of broadly rounded tip. The *Addisonia* protoconch is very similar in both shape and sculpture to those in the pseudococculinid genera *Kurilabyssia* Moskalev, 1976, and *Mesoplex* Mar-shall, 1986, while that in *Helicopelta* is similar to those

in Choristellidae and Cocculinoidea in shape (Marshall, 1986; McLean, 1992).

On aggregate character states *Helicopelta* is as different from all families and subfamilies of Lepetelloidea as they are from each other, which suggests that it may represent a family in its own right. Without a thorough re-evaluation of phylogenetic relationships within the superfamily, however, particularly in the light of knowledge of the anatomy of *Helicopelta* (unknowns), I favor a conservative approach and allocate it subfamilial rank within Addisoniidae, associating it there solely on the basis of similarity of the radula to that of *Addisonia*. The existence of a group of operculate, coiled species related to *Addisonia* is scarcely surprising, since Haszprunar (1988b, 1992) has already provided compelling evidence that Addisoniidae and Choristellidae are probably sister groups.

**Etymology:** Greek *helikos* (spiral) and *pelte* (shield)—feminine.

*Helicopelta* Marshall, gen. nov.

Type species: *Helicopelta rostricola* Marshall, sp. nov.

**Diagnosis:** As for *Helicopeltinae* (above).

*Helicopelta rostricola* Marshall, sp. nov.

(Figures 1–8, 13–18)

**Description:** Shell (holotype) 1.90 mm wide, turbiniform, slightly wider than high, thin, spire  $0.2\times$  as high as aperture, umbilicus small, translucent; periostracum thin, smooth, pale buff.

Protoconch 200  $\mu\text{m}$  wide, sharply delineated, slightly tilted, entire surface with minute, densely crowded, sharp-edged pits.

Teleoconch of two rapidly expanding convex whorls, suture narrowly channelled, smooth apart from collabral growth lines, and a few obscure spiral lines on last quarter whorl. Aperture very large, roundly “D”-shaped, peristome continuous, inner lip flared and obscuring umbilical chink from basal view.

Animal (Figures 5–8) white, eyeless. Head broad, broadly rounded; snout broad, bluntly truncated; oral shield broad, mouth “Y”-shaped, no oral lappets. Cephalic tentacles similar, short, bluntly tapered. Copulatory organ hemispherical, set close below left cephalic tentacle, opening not detected. Gill attached to pallial roof, comprising 12 leaflets, long, arcuate, curving anterolaterally from left side to right of body midline. One slender posterior epipodial tentacle on each side beside opercular lobe. Foot large, spongy, oval, wider than long; with a narrow, laterally elongate projecting subcentral area. Shell muscle horseshoe-shaped, uninterrupted, broad, ends very broad. Jaws lacking.

Operculum extremely thin, fragile, firmly attached, col-

orless, transparent, nucleus slightly eccentric, similar to that in *Choristella*.

Radula (Figures 13–18) with the formula  $11 + 5 + 1 + 5 + 11$ . Central and lateral teeth short, topographically complex, complexly interlocking, central and inner four laterals without defined cutting areas or cusps. Central tooth low, scalelike, subquadrate, medially thickened, sides thin and laterally flanged. Laterals 1–3 trapezoidal, tile-like, enlarging outward. Lateral 4 small, shorter than flanking teeth, inconspicuous, tip subangulate. Lateral 5 broad, a narrow hooked cusp on narrow inner part, broad; low outer part completely obscured by marginal 1, base strongly flanged and deeply socketed to interlock with marginal 1. Marginal 1 very large, base tightly locked between lateral 5 in its own row and the row in front, about as broad as lateral 5, with four strong, bluntly angulate or rounded, similar cusps. Marginal basal plates thin, scalelike. Outer marginal teeth small, slender, no longer than marginal 1, 10 per half transverse row, tips finely serrate.

**Type data:** Holotype MNHN (height 1.80 mm, width 1.90 mm, 2 teleoconch whorls); MUSORSTOM 5 station 363,  $19^{\circ}48'S$ ,  $158^{\circ}44'E$ , Chesterfield Plateau, Coral Sea, alive on inner side of a detrital cephalopod beak pitted by bathysciadiids, 700–685 m, 19 October 1986, n.o. *Coriolis* (according to the label, two specimens were originally present, but the second specimen could not be located).

**Distribution:** Chesterfield Plateau, Coral Sea, 700–685 m.

**Remarks:** *Helicopelta rostricola* is strongly characterized by its small, coiled, operculate shell, external anatomy, radula, and association with cephalopod beaks. It remains to be determined whether or not the protoconch naturally has an external organic layer (as in the species described below) that has been abraded away in the holotype.

**Etymology:** Latin *rostrum* (beak) and *cola* (dweller).

*Helicopelta* sp. nov.

(Figures 9–12)

**Description:** Shell (immature) up to 0.60 mm wide, wider than high, almost planispiral, thin, brittle, colorless, translucent, narrowly umbilicate; periostracum pale buff, translucent, essentially smooth.

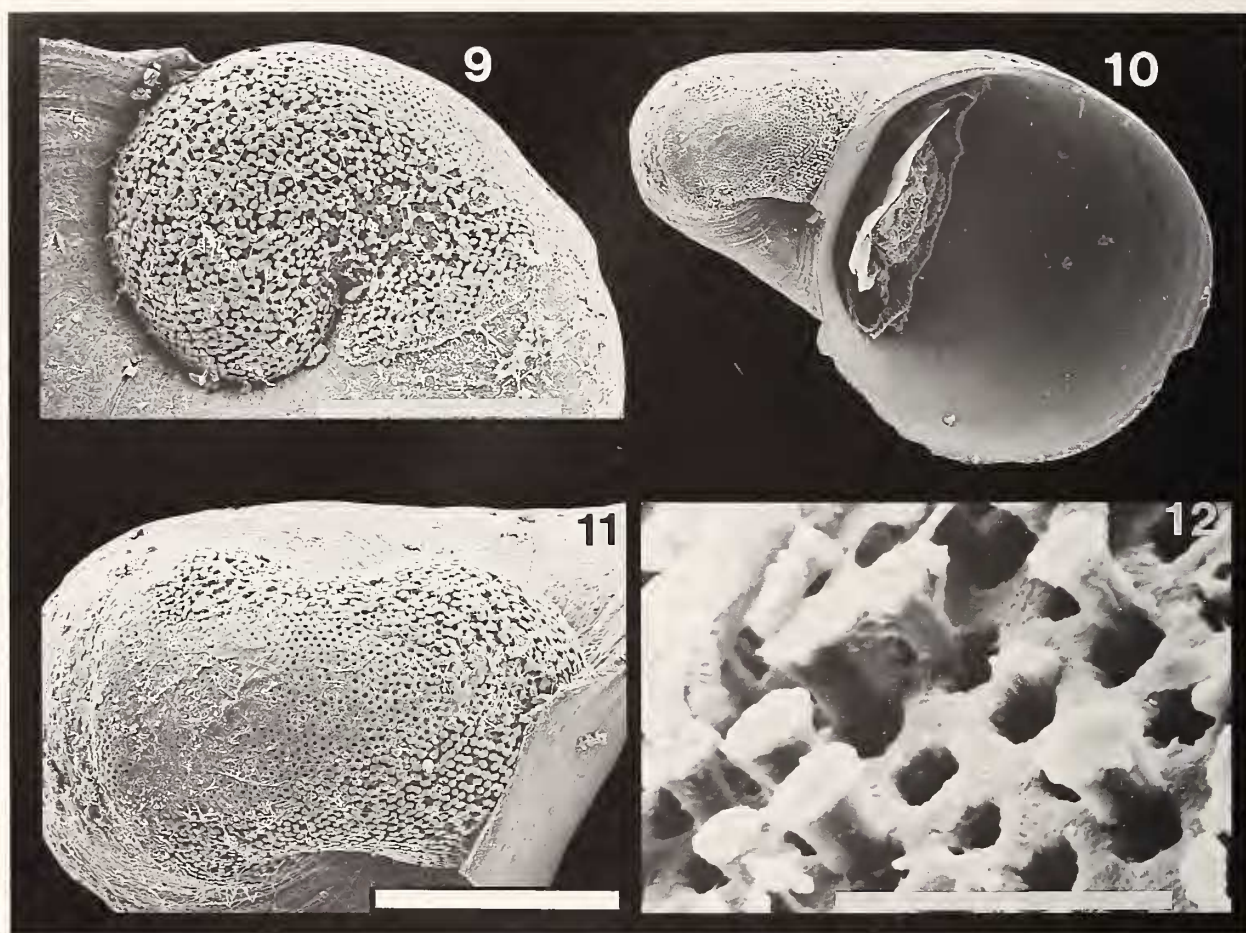
Protoconch 200  $\mu\text{m}$  wide, sharply delineated, orthostrophic, covered with minute, crowded, sharp-edged pits; where unabraded, each pit with a stout column with a broader, flattened top that projects above surface (apparently dried, shrunken outer organic layer).

Teleoconch of about half a whorl, suture deeply impressed, smooth apart from growth lines, rapidly expanding, summit above tip of protoconch; aperture circular.

Animal unknown (dried). Operculum very thin, chitinous, colorless, spiral.

**Material examined:** CHALCAL 2 station CP22,  $24^{\circ}40'S$ ,





Explanation of Figures 9 to 12

Shell of ?*Helicopelta* sp. nov. (immature), off southern New Caledonia, 750 m. Figures 9, 11. Protoconch. Figure 10. Whole shell (width 0.60 mm), note operculum in place. Figure 12. Enlargement of protoconch sculpture. Scale bars 5, 7 = 100  $\mu$ m, 8 = 10  $\mu$ m.

168°39'E, southeast of New Caledonia, alive on inner side of a pitted detrital cephalopod beak with *Bathysciadium* sp., 750 m, 29 October 1986, n.o. *Coriolis* (2 juveniles MNHN).

**Remarks:** The two available specimens are clearly immature (largest shell 0.60 mm wide). They resemble *H. rostricola* in protoconch size, in gross teleoconch facies, and in opercular morphology, but differ in having a strongly flattened spire. The protoconch surface is pitted exactly as in *H. rostricola*, but differs in that stout, nail-like columns project from the pits. Nothing like them has been previously recorded from Cocculinoidea or Lepetelloidea. Judging from the fact that the columns are narrower than the pits and stuck to their sides, they seem likely to represent the dried, shrunk remains of an organic layer that is impervious to salts secreted during mineralization of the protoconch. The columns are clearly fragile and easily removed by abrasion (Figures 5, 7, 8). There is no trace

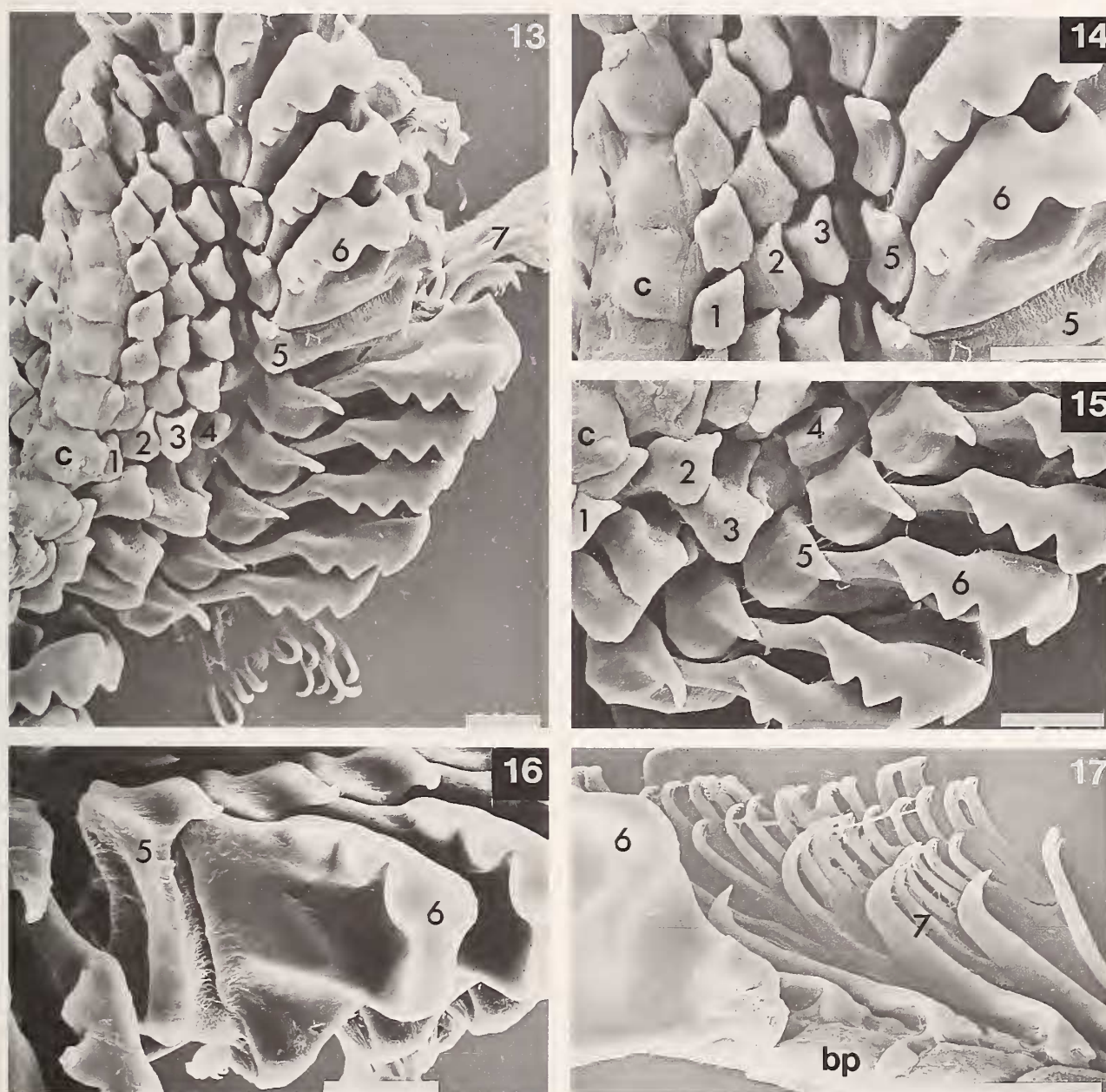
of them on the protoconch of *H. rostricola*, and it is yet impossible to tell whether or not they were present and have since worn away. The similarities and the association with a cephalopod beak suggest that it is a species of *Helicopelta*, naming of which is withheld until better material is available.

#### Family PSEUDOCOCCULINIDAE Hickman, 1983

##### Genus *Tentaoculus* Moskalov, 1976

*Tentaoculus* Moskalov, 1976:67. Type species (by monotypy): *Tentaoculus perlucida* Moskalov, 1976; Recent, New Guinea.

**Remarks:** Since the discovery of *Tentaoculus perlucida* Moskalov, 1976, off New Guinea (substratum unknown), three species have been described from off New Zealand (Marshall, 1986): *T. lithodicola* and *T. neolithodicola* from the carapaces of living stone crabs (Crustacea: Lithodidae),



Explanation of Figures 13 to 17

Radula of holotype of *Helicopelta rostricola* Marshall, gen. nov., sp. nov. Figures 13–17. Central tooth (c), lateral teeth (1–5), and marginal teeth (6, 7) of right side of radular ribbon. Figure 16. Lateral 5 (5) and marginal 1 (6). Figure 17. Marginal 1 (6), marginal basal plates (bp), and slender outer marginal teeth (7). Scale bars = 10  $\mu$ m.

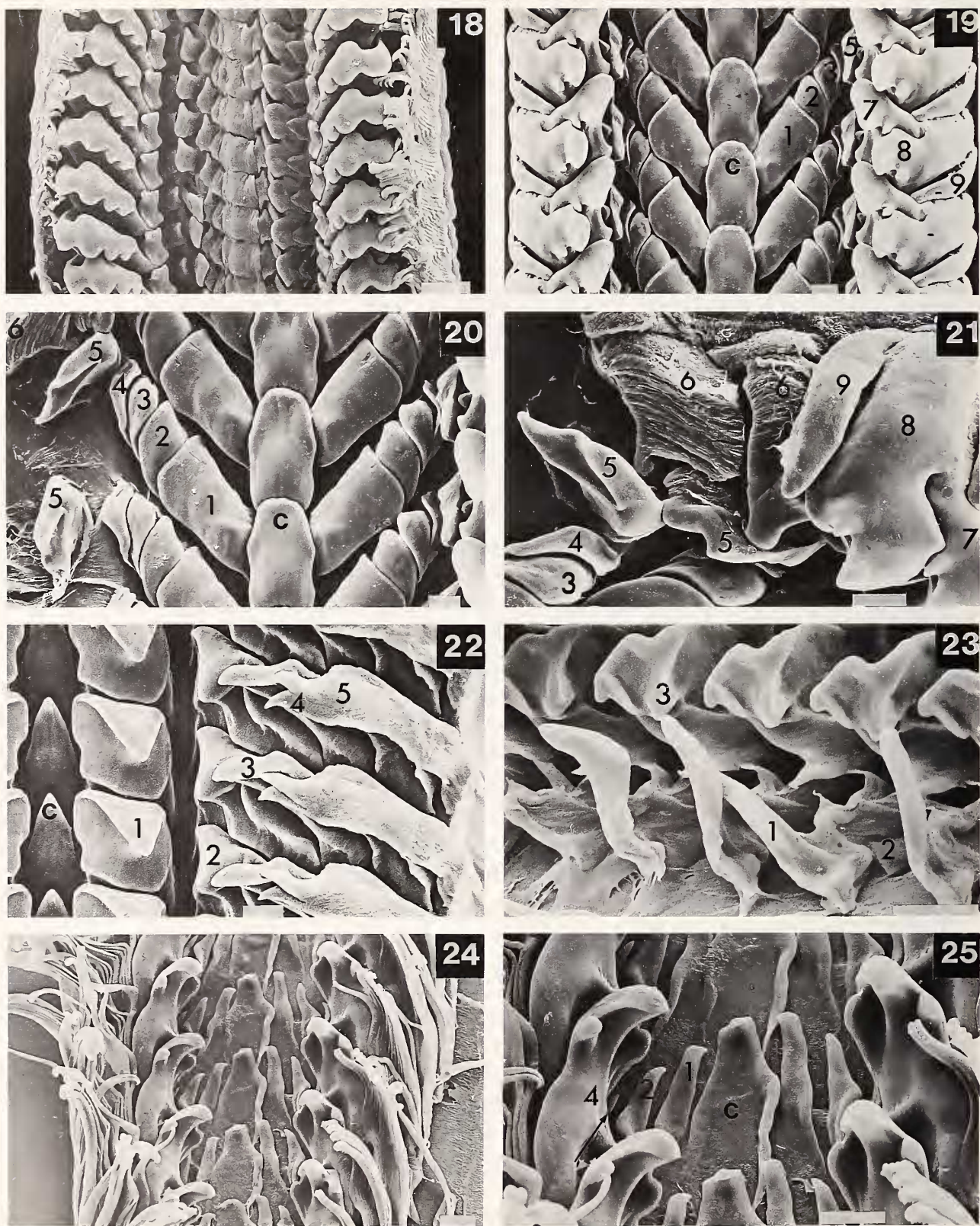
and *T. haptricola* from decaying algal holdfasts at bathyal depths. The North American species *Puncturella* (*Fissurisepta*) *eritmeta* Verrill, 1884, *Cocculina georgiana* Dall, 1927 have been referred to the genus by McLean & Harsenewych (1995) on the basis of shell morphology. The new species described below is the first record of a pseudococculinid living in association with chondrichthyan egg cases.

*Tentaoculus balantiophaga* Marshall, sp. nov.

(Figures 26–28)

**Description:** Shell up to 3.25 mm long, thin, translucent, white, moderately arched, anterior end occupying 82–88% of shell length. Aperture elliptical, broadest at about anterior third, more or less flat. Anterior end more broadly





#### Explanation of Figures 18 to 25

Figure 18. Full width of radula of holotype of *Helicopelta rostricola* Marshall, gen. nov., sp. nov. Figures 19–21. Radula of *Addisonia* sp. nov., off Shoalhaven Heads, New South Wales, 494–585 m, AMS C. 200901, showing central tooth (c), lateral teeth (1–5) and marginal teeth (6–9). Figure 19. Full width. Figures 20, 21. Details. Figure



rounded than posterior, sides broadly rounded. Anterior slope broadly convex, posterior slope concave, lateral slopes more or less flat. No internal septum.

Protoconch sculpture unknown (surface etched away).

Teleoconch sculptured with fine collabral growth lines.

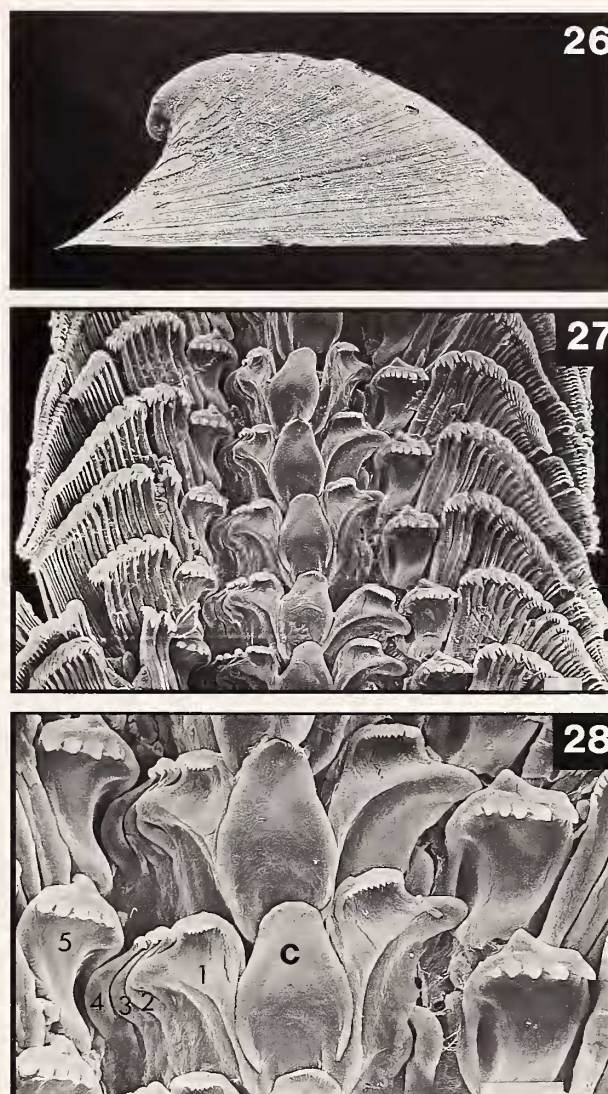
Animal translucent white, eyes unpigmented, snout broadly rounded, cephalic tentacles gently tapered and similar, oral disc broad, two posterior epipodial tentacles; narrow seminal groove entering base of right cephalic tentacle.

Radula (Figures 27, 28). Radular formula  $\infty + 5 + 1 + 5 + \infty$ . Central tooth with broad, rounded, obscurely serrate cutting area. Lateral 1 large, cutting area broad, straight, outermost cusp large, inner edge with six to nine small conical cusps. Lateral 2–4 small, each with strong, hooked terminal cusp, and one to three small secondary cusps. Lateral 5 largest, broad, straight cutting area with four to seven strong conical cusps. Marginal teeth numerous, slender, tips finely serrate.

**Type data:** Holotype NMNZ M.118318, and 6 paratypes (1 AMS, 5 NMNZ M.117577): 41°07.61'S, 176°46.91'E, off Castlepoint, New Zealand, alive within spent skate egg case, 1335 m, 2 April 1993, f.r.v. *Tangaroa* sta. 9303/149, coll. P. Grimes. Paratypes (13 NMNZ M.117836, 1 AMS, 1 MNHN): 44°13.47'S, 178°41.87'E, western Chatham Rise, New Zealand, alive within spent skate egg case, 1065–1072 m, 8 November 1993, f.r.v. *Tangaroa* sta. 9309/197, coll. A. Hart.

**Distribution:** Off Castlepoint, and western Chatham Rise, New Zealand, living within and feeding on spent skate egg cases, 1065–1335 m.

**Remarks:** The shell, radula and external anatomy of *Tentaoculus balantiophaga* are typical of the genus *Tentaoculus* as defined by Marshall (1986) and Haszprunar (1988a). *T. balantiophaga* differs from *T. perlucida* in lacking eye pigment, and in having a more strongly developed central tooth. It differs from *T. haptricola* in lacking an internal shell septum, and from both *T. lithodolica* and *T. neolithodolica* in having finer cusps on lateral 1, and fewer and shorter cusps on laterals 2–4. *T. balantiophaga* is unique among Cocculiniformia associated with cephalopod beaks and chondrichthyan egg cases in that the radula exhibits no obvious derived character states (see below). Other egg cases from the vicinity contained *Choristella marshalli* McLean, 1992, and the two species have not been found living



Explanation of Figures 26 to 28

Holotype of *Tentaoculus balantiophaga* Marshall, sp. nov., off Castlepoint, New Zealand, 1335 m. Figure 26. Shell, length 2.55 mm. Figure 27. Full width of radula. Figure 28. Detail of radula showing central tooth (c) and lateral teeth (1–5). Scale bars = 10  $\mu$ m.

22. Detail of radula of paratype of *Choristella marshalli* McLean, 1992, off Banks Peninsula, New Zealand, 1097–1116 m, NMNZ M.75210, showing central tooth (c) and lateral-marginal teeth (1–5). Figure 23. Oblique lateral view of right side of radula of syntype of *Bathysciadium costulatum* (Locard, 1898), MNHN, showing innermost three lateral teeth (1, 2, 3). Note that the tip of (numbered) lateral 1 locks into the socket on the inner side of (numbered) lateral 3 in the row in front. Figures 24, 25. Radula of paratype of *Teuthirostria cancellata* Moskalov, 1976, off northern Peru, 5540–5200 m, Academy of Sciences, Moscow. Figure 24. Full width, note low number of marginal teeth. Figure 25. Detail showing central tooth (c) and lateral teeth (1–4; tooth 3 obscured, tip arrowed). Scale bars = 10  $\mu$ m.



together within the same egg case. *T. balantiophaga* forms grazing scars on the inner surface of the egg cases similar to those produced by *Choristella* and *Addisonia* species.

**Etymology:** From the Greek *balantion* (purse) and *phagos* (to eat), the word *balantion* alluding to "mermaid's purse," a common name for chondrichthyan egg cases.

## DISCUSSION

There is compelling evidence that gastropod limpets are derived from coiled forms (Yonge, 1947; Eales, 1950; Fretter & Graham, 1962; McLean, 1981, 1984; Lindberg, 1988), though Haszprunar (1988b, c, 1992) considered the uncoiled limpet form to be primary and coiled forms secondary in gastropod evolution. On the basis of outgroup comparison (Pseudococculinidae and/or Osteopeltidae), Haszprunar (1988b, c, 1992) concluded that Choristellidae were not phylogenetically primitive among Cocculinoidea and Lepetelloidea, and that coiling in this particular family must thus be a derived condition. The presence of a relatively huge, horseshoe-shaped shell muscle in *Helicopelta* suggests derivation from a limpet ancestor and lends support to this contention. It is unclear, however, whether the shells in Choristellidae and *Helicopeltinae* have become coiled independently.

It is difficult to imagine an advantage that might be conferred through reacquisition of a coiled shell other than increased mobility. Why secondary coiling should have occurred in Choristellidae and *Helicopeltinae* alone among Lepetelloidea is unclear, though it is perhaps no coincidence that these groups are the only ones to be entirely dependent on chondrichthyan egg cases and cephalopod beaks for food other than Bathysciadiidae, *Teuthirostria cancellata* Moskalev, 1976 (Cocculinidae), and *Tentaoculus balantiophaga* sp. nov. (Pseudococculinidae) (see below), all of which have patelliform shells. Judging from first-hand sorting of more than 1000 dredge and trawl samples from depths greater than 500 meters (personal observation; P. Bouchet & A. Warén personal communication), beaks, egg cases, bones, wood and algal holdfasts are generally rare, and must be so thinly distributed over most of the seafloor that these animals probably do not depend on an ability to crawl from one substratum to another. *Helicopelta* species presumably utilize the substratum between more sedentary (scar-forming) bathysciadiids, or perhaps areas formerly occupied by the limpets. A coiled shell may enhance reproductive fitness by enabling animals to seek parts of the original substratum following its ultimate disintegration and scattering of the parts or, for the choristellids, perhaps other egg cases deposited in the immediate vicinity.

*Helicopelta rostricola* joins the limpets of the Bathysciadiidae (= Bathypeltidae) (Moskalev, 1973; Hickman, 1983; Haszprunar, 1987b), and the cocculinid limpet *Teuthirostria cancellata* Moskalev, 1976 (Moskalev, 1976) as the only gastropods known to live and feed on the beaks of cephalopods, while *Tentaoculus balantiophaga* joins Addisoniidae and Choristellidae as the only gastropods known

to live and feed within the egg cases of sharks and skates (Verrill, 1882, 1884; Villa, 1985; McLean, 1985, 1992; Gubbioli & Nofroni, 1986).

Warén (1993) has recently introduced a new limpet genus, *Xenodonta*, which he tentatively referred to Bathysciadiidae. Whereas he could not record the diet of the North Atlantic type species (*X. bogasoni* Warén, 1993), an undescribed species from the Galapagos Islands was reported to live and feed on the periostracum of a species of *Capulus*. Compared with *Bathysciadium*, the radula in *Xenodonta* differs in lacking the low articulatory tooth (tooth 2, Figure 23) between the bases of laterals 1 and 3, in that lateral 2 (Warén's tooth 3) is more like that in *Lepetella* Verrill, 1880 (Lepetellidae), and in having an extra pair of outer lateral teeth.

The external anatomy and radula of *Teuthirostria cancellata* (paratype, off northern Peru, 5540–5200 m) (Figures 24, 25) are accordant with Cocculinidae, though serial sections reveal some deviations from the standard cocculinid plan (G. Haszprunar, personal communication). Moreover, the radula has substantially fewer marginal teeth per transverse row (about 23 pairs) than any other known cocculinid. The lower number of marginal teeth suggests that the radula has undergone or is undergoing a progressive morphological transformation, presumably through retardation of radular ontogenesis. Regrettably, the shell of the only specimen available to me had dissolved in its preservative, so it was not possible to check the protoconch, which was described as being smooth (this requires confirmation as the protoconch surface is not in fact shown in the original illustration—Moskalev, 1976: fig. 3).

Cephalopod beaks are composed of chitin, a polysaccharide with long fibrous molecules. By contrast the egg cases of sharks and skates are composed primarily of layers of the structural protein collagen (Wourms, 1977; McLean, 1985). Gastropod periostracum comprises largely sclerotized fibrous protein (Hochachka, 1983; Saleuddin & Petit, 1983). How these tough, almost inert substances are metabolized is unknown, though it is possible that endosymbiotic bacteria are involved. All that can be said at present is that the animals exhibit certain derived features in their alimentary tracts: bathysciadiids have a large stomach and have lost the midgut gland, which has been functionally replaced by a greatly enlarged esophageal gland; choristellids lack a gastric shield and have a specific gland at the posterior esophagus, large "cul-de-sacs" (probably the midgut gland), and a short intestine; *Addisonia* species have entirely lost the stomach and have it replaced by a greatly enlarged intestinal sac (Haszprunar, 1987a, 1988b, 1992).

Aside from the strong probability that larvae in Cocculinoidea and Lepetelloidea are non-planktotrophic (as in all known archaeogastropods other than Neritimorpha), nothing is known of the development of these animals. Given the fact of their ability to colonize static, widely scattered, ephemeral substrata, it seems obvious that this is accomplished by transportation of eggs or larvae in cur-

rents close to the seafloor, settlement occurring when the presence of food is detected, probably by chemoreception. Brood protection of yolk-rich eggs has been reported for a number of families (Haszprunar, 1988b). Retention of eggs to a late stage of development would maximize exploitation of the substratum, whereas yolk-richness would enhance long-term survival during larval dispersal.

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